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ON THE MECHANICAL GENESIS OF TOOTH-FORMS.

BY JNO. A. RYDER.

During a study of the osteology of the mammalia, the views herein advanced were first conceived as a rational explanation of the origin of the shapes of dental structures, as they exist in the different groups. More mature deliberation has only served to strengthen the conviction that the inquiry is in the right direction, since no body of facts with which I am acquainted are more beautifully and intimately interrelated than those which I have here so imperfectly presented. It is hoped that a better appreciation of what might, without violence to commonly received ideas, be called evolutionary teleology, may be attained by pursuit of similar inquiries in other directions.¹ This attempt to unravel a portion of the complex interrelations of the parts of organic beings, so as to show how their metamorphoses may be effected by mechanical means, it is believed, may not strike the mind of the reader as altogether futile, nor the title as quite so presumptuous, as would at first appear, after all the facts have been weighed. The interpretation of the rationale of the differentiation of structures in a mechanical way is not entirely new, since Lamarck, in his "*Philosophie Zoologique* (1809), and latterly Mr. Spencer, with greater philosophical grasp, have both shown that efforts exerted to overcome resistances are retroactive and induce modifications in the parts of organisms.²

¹ Am. Naturalist, 1877, p. 603. Nature, vol. 17, 1877, p. 128.

² It may be observed here that the nomenclature of tooth-forms adopted throughout is that proposed by Prof. E. D. Cope in his memoir, entitled "On the Homologies and Origin of the Types of Molar Teeth of Mammalia Educabilia (Journ. Acad. Nat. Sci., Philada. 1874). The names are not intended as characterizing groups or orders in the system, but rather as distinguishing distinct classes of teeth, which may exist in the same or nearly the same form in several distinct orders or families of the class. The definitions of terms remain the same, except those of the words *isognathous* and *anisognathous*, which I use so as not only to indicate respectively parity and disparity in transverse diameter of the crowns of the upper and lower molars, but also the parity or disparity in width transversely, from outside to outside, over both maxillaries, including the bony palate and the width across both rami of the submaxillary. This additional signification

Tooth-forms and Jaw-movements of the Groups.—It may be stated in general terms that the primates are bunodont and relatively isognathous, consequently the lateral movement is limited. This type of dentition is affirmed to be generalized, or, in other words, to be present in several diverse groups; first occurring in earlier forms and in the young of many, previous to or during the protrusion of the teeth from the gum, prior to or about the time they become functional. Man is usually not perfectly isognathous, the nearest approaches to it that I have observed were in the skulls of a Slavonian and an Anglo-Saxon. *Cynopithecus* and *Macacus* are anisognathous, and the South American howler monkeys and marmosets even more so. The American primates seem to present the anisognathous extreme, and the Old World forms the isognathous. Another fact of interest here is the shape of the glenoid cavity. In the gorilla it is more like man's than in any primate I have examined; deeply excavated transversely, with a prominent transverse ridge bordering the excavation anteriorly. This form of glenoid cavity entirely disappears in the howlers, in which it is a comparatively plane surface; the superior surface also of the condyle is flattened and expanded transversely, as in selenodont ungulates, which agrees with the presence of the rudimentary crescentic cusps and the anisognathism. The chimpanzee has a relatively plane glenoid surface, and in man the depth of the excavation of the cavity is greater even in the Australian, the lowest modern type of human skulls.

The dentition of *Feræ* is bunadont, usually somewhat anisognathous, the tubercles are laterally compressed, with edges so sharp as to constitute a very effective apparatus for cutting the tough tendons, ligaments, and bones of their prey. The mandibular articulation is the most perfectly ginglymoid in the class, and hence also admits of the least lateral movement. All the lateral movement observable is that which is effected by the lateral sliding of the cylindroid condyles in the glenoid cavities; the effect is, however, widely different from the lateral movement observed in ungulates. In these the distal end of the mandible moves through the greatest space, while in *Feræ* all points of the

slightly changes the proposed grouping in the memoir referred to, but it also has the greater advantage of making words already in use serviceable and analogous in meaning to *prognathous* und *orthognathous*, as first used by Retzius in craniography.

jaw in sliding sidewise pass through the same distance. A few of the group retain the simple haplodont type of tooth, *e. g.*, *Rosmarus*.

The passage from the archetypal bunodont tooth to the scissors-like (carnassial) sectorial arrangement is plainly exhibited, by selecting a series beginning with *Ursidæ*, and continuing with *Amphicyon*, *Procyonidæ*, *Melinæ*, *Cercoleptes*, *Mustelidæ*, etc., and ending with the *Felidæ*, as the extreme of specialization.

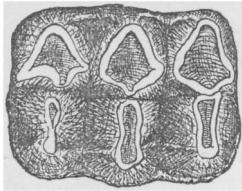
Amongst the *Ungulata*, the most conclusive evidence is found in confirmation of the law of dental modification here enunciated. The numerous living and extinct species present a remarkable chain of dental forms, gradually departing from the bunodont type, and passing into the excessively modified selenodont, accompanied with increased mobility of the mandible in a lateral direction and increased anisognathism.

The *Toxodontia* present a ptychodont type of dentition, are very anisognathous, and the condyles approach in form those of the selenodont ungulates; they in all probability moved their jaws laterally. The enamel patterns are reversed in opposite series.

The Hyracoidean dentition is tapirodont, with an apparent tendency towards the selenodont, anisognathous with condyles transversely expanded, which may be regarded in connection with the truncate crowns of the molars and plane condyles as evidence of extensive lateral movement.

The *Proboscidea* are regarded as trichecodont, a careful examination, however, reveals that the inner tubercles above and the

Fig. 1.



Right upper molar of *Mastodon*.

outer ones of the inferior molars of some of the extinct forms (*Trilophodon* and *Tetralophodon*) were slightly selenodont (Fig. 1), anisognathous; molars tuberculate, in few cross crests; condyles more like that of selenodont ungulates, with lateral motion. In *Elephas* and *Loxodonta* the jaw-movement is from behind forwards; condyles more rodent-like, isognathous; molars with flat crowns; tubercles becoming obsolete from wear, and blended into numerous transverse plates.

The *Sirenia* are trichecodont and bunodont. The trichecodont form (*Manatus*) seems to have some lateral motion, as there is

some degree of anisognathism. The teeth of the Dugong when young are bunodont, as is shown by a specimen in the collection of the Academy.

The toothed cetaceans have a type of dentition more or less nearly haplodont (*Zeuglodon* presents two rooted molars and premolars, with a simple, compressed serrated crown).

The *Mysticete* are without true teeth, jaws greatly modified, rami separate, keratose laminae (baleen) and surrounding soft parts acting as a prehensile apparatus in connection with the movement of the creature through the water.

In the insectivorous group *Chiroptera*¹ the dentition approaches, in some respects, that designated as symborodont. It is anisognathous, but differs in the bats from the symborodont greatly in the manner in which the teeth of opposite series fit into each other; it is also met with in nearly as marked a form in some marsupials (*Didelphys*), and in *Insectivora* (*Talpidae*, etc.). The anterior V-like cusp of the inferior molar series is longer than the posterior, the former fits into an acute or triangular space partially separating the upper molars on the inside, the latter fits

¹ The following tables are of interest as exhibiting a gradual reduction of molars and premolars in this group. They are taken from an abstract of an elaborate paper by W. Leche in *Weigmann's Archiv f. Naturges.* xliii., Pt. 5, 1877, 353. I have not seen the original in *Lund's Universitets Arsskrift*, tome xii., 1876:—

I. Showing gradual loss of posterior molars in the Phyllostomata and Desmodina—

<i>Brachyphylla</i> ,	}	pm. $\frac{2}{3}$	m. $\frac{3}{3}$ (fully developed upper 3d m.).
<i>Sturnira</i> , etc.,			m. $\frac{3}{3}$ (rudimentary upper 3d m.).
<i>Artibeus</i> ,			m. $\frac{2}{3}$.
<i>Chiroderma</i> ,			m. $\frac{2}{3}$ (fully developed upper 2d m.).
<i>Pygoderma</i> ,			m. $\frac{2}{3}$ (rudimentary upper 2d m.).
<i>Diphylla</i> ,			m. $\frac{1}{3}$.
<i>Desmodus</i> ,			m. $\frac{0}{3}$.

II. Showing gradual loss of middle premolars in the Vespertilio series—

<i>Vespertilio</i> , pm. $\frac{3}{3}$	}	m. $\frac{3}{3}$	$\left(\frac{\text{pm. } 1 + 2 + 3}{\text{pm. } 1 + 2 + 3} \right)$
<i>Plecotus</i> , pm. $\frac{2}{3}$			$\left(\frac{\text{pm. } 1 + 3}{\text{pm. } 1 + 2 + 3} \right)$
<i>Vesperugo</i> , pm. $\frac{2}{2}$			$\left(\frac{\text{pm. } 1 + 3}{\text{pm. } 1 + 3} \right)$
<i>Vesperus</i> , pm. $\frac{1}{2}$			$\left(\frac{\text{pm. } 3}{\text{pm. } 1 + 3} \right)$

into a similar space or groove, between the V-like cusps of the upper molars. The condyles are elongated transversely and somewhat ginglymoid in respect to articulation, and do not admit of much lateral movement.

The foregoing remarks render further notice of the dentition of *Insectivora* unnecessary, or see St. G. Mivart's papers.¹

Amongst Rodents a greater variety of dental forms is to be found than in any other order of the class with the exception of the marsupials; frequently haplodont, ptychodont, or bunodont, and, sometimes, even approaching the selenodont form. It is very likely that the very common opposite arrangement of the folds of enamel in the opposite series has had the same origin as those in the selenodont system. In many species the dentition is peculiar, and has no parallel in other orders. What is now referred to is the curious pattern met with in such genera as *Arvicola*, *Fiber*, and *Neotoma*, where the figure formed by the enamel covering of the triangular dentine columns stands reversed in respect to those of their fellows of the opposing series. The various grades of anisognathism and isognathism here find their fullest expression; indeed, the multiformity in this and other features is such as to be worthy of more extended study than can be devoted to them without a complete collection of jaws and teeth of recent and fossil species.

The dental system of *Bruta* is usually haplodont, though in the extinct *Hoplophoridæ* and *Myodontidæ*, it was ptychodont in form, but not in structure, since there was no enamel to be folded. In the former group (*Glyptodon*) the teeth were inclined forwards in the lower series, and backwards above, as observed in Arvicoline rodents, which with their form in section gives us a hint as to the origin of that form.

The marsupials, other than the insectivorous ones, present the trichodont and a type simulating the selenodont in *Phascalomys*. A remarkable form is observed in *Stereognathus*, as described by Owen, where the crescentoid middle tubercles have the convex side directed backwards, and the concave forwards in the molars of the mandibles, which arrangement, as he observes, is not found in any other living or extinct species of mammal.

¹ Journ. of Anat. and Physiology, vol. i., 1867, pp. 280-312; Ib. vol. ii. pp. 117-154.

Differentiation of Dental Systems.—By what Professor Cope calls “synthesis of repetition,”¹ the origin of the various types of mammalian dentition is rationally accounted for, by supposing an additional modicum of growth force as duplicating the primitive dental body, in lateral, longitudinal, or oblique directions. In all the ruminating ungulates the repetition of tubercular structures is now tending to take place on those sides of the teeth most subject to the severe impacts incident to mastication, as is shown by the appearance of rudimentary tubercles (cingules) upon the outside of the molar teeth in the mandible, and upon the inside in the molars of the maxillary. Another kind of differentiation has taken place in the incisors of the horse, as I have attempted to show in a previous paper,² where the duplication has taken place from the posterior side, in accordance with the generally prevalent acceleration going on in the whole dental system, and to account for which I cannot forbear suggesting that the severe wear to which these structures have been so long subject, together with the peculiarities of mandibular motion, have conspired to produce the following changes: the elongation of the teeth, their consequently deeper implantation in the mandible, and the fusion of the fangs or roots into the simple, persistently growing, rootless columns. This gradual elongation and fusion of the roots of the teeth is well seen in the series of horses’ teeth which Prof. Huxley presents in his third lecture in New York. There are also instances amongst Artiodactyls, the great *Edentata* (*Megatherium*), many herbivorous rodents, elephants, etc., in all of which it is noticed that the later forms are invariably possessed of the longest teeth growing from more or less distinctly persistent pulps, or some arrangement which is equivalent. These forms with the long molars have almost invariably been herbivorous with lateral motion of the mandible, while the short unmodified tubercular form of molar tooth with fangs has been preserved in those types in which the food was already pre-

¹ Proc. Am. Philos. Soc., 1871, p. 242.

² Proc. Acad. Nat. Sci., Phila. 1877, p. 152. I have since observed an instance in an incisor of *Cynopithecus*, where the prominent cingulum on the posterior face of the tooth came very near being functional, so as to inclose an area homologous with the “mark” or cul-de-sac in the incisors of the horse, proving conclusively to my mind that such has been the origin of the complex incision of the latter animal.

pared for assimilation, or was relatively soft as in the *Suina* and some rodents (*Sciurus* and *Mus*). In all rodents, the incisors grow from persistent pulps, no matter whether the molars grow from such pulps or not, showing again that strains have here played the part of directive agents, controlling growth force.

Methods of cusp duplication may be tabulated as follows:—

1. Interstitial ; developing connecting ridges (possibly this appearance is often due to compression of the cusps).
2. Lateral ; either palatal or buccal, internally above, and externally below (*Cervus*, *Bos*).
3. From behind ; by the successive addition from behind of transverse rows of cusps or greatly flattened and expanded single ones. As in *Mastodon*, *Elephas*, *Hydrochoerus*, and *Potamochoerus*.

Whilst such changes in cusp growth are going on, the external cementum layer thickens as modern and domesticated forms are approached ; the last (living) term in a given phylum of herbivorous ungulates usually having it thickest.

Prof. Harrison Allen's views on cusp duplication, as expressed in an article in the *Dental Cosmos*,¹ "On the Nomenclature of the [human] Teeth," are worthy of notice in this connection. His views, which are very clearly stated, may be summarized and somewhat expanded, so as to include other mammalia, as follows:—

1. That the cusps are the initial (embryological, and, therefore, palingenetic) elements of the teeth from which the fangs or roots are produced by the gradual thickening of the dentinal structures.
2. That the development of bicuspid (premolar), quadricuspid (molar) teeth is effected by the repetition of the unicuspid form (incisive or haplodont), *i. e.*, by the functional development of Cingules,² or rudimentary cusplets at the base of the crowns of unicuspid, bicuspid, quadricuspid, etc, forms, often forming cingula, that are frequently broken up into small, more or less distinctly defined tubercles.

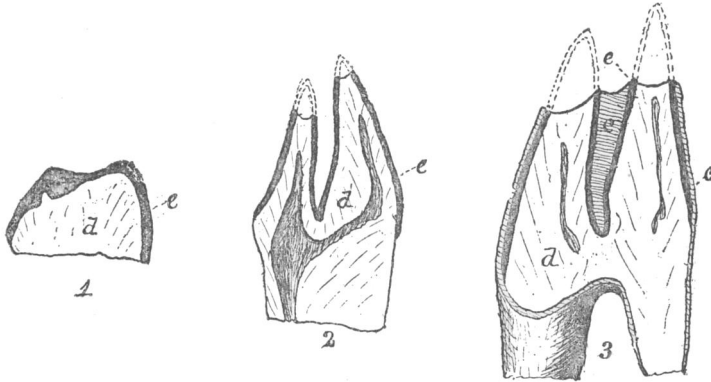
Several instances occur amongst the mammalian orders exhibiting greatly elongated cusps. In the cases of the Ungulates and Proboscideans the steps of the process can be pretty easily traced. In the former the primary form is the simple cone, which gradu-

¹ Vol. xvi., 1874, pp. 617-623.

² A convenient term, proposed by Prof. Allen.

ally becomes more and more compressed, and at the same time produced (Fig. 2), the acute fore and aft edges of which are turned

Fig. 2.



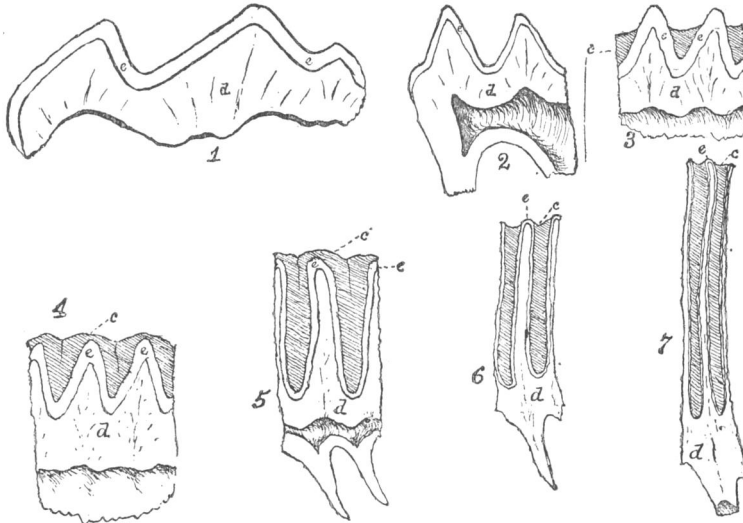
1. Transverse vertical section of rear upper molar of *Sus erymanthus*.
2. Same of *Tragocerus amaltheus*.
3. Same of *Bos taurus* (Altered from Gaudry). *d*, Dentine; *e*, enamel; and *c*, cementum. The dotted lines at the apices of the cusps of 2 and 3 show the portion worn away.

either outwards or inwards, as the teeth happen to be upper or lower molars, while as the apical portion of the cusp is worn off the characteristic crescentoid pattern becomes apparent.

In the Proboscidiæ we probably encounter a successional series of tooth forms in which the individual cusps were short and distinct, with little cementum in *Mastodon*, but as the surviving group of true elephants is approached both the recent species and the extinct species allied to them exhibit a great production of the tubercles, while, as we should expect, they at the same time become much more numerous. The enamel is the only considerable covering of the crowns in the cusped forms, whereas in the forms with lamellate teeth the transverse sulci (valleys), are gradually deepened and filled with cementum, which constitutes about half of the mass of the teeth in some instances. In the milk dentition of *Loxodon africanus* evidence of the original bi-tuberculate condition of the lamellæ (tubercles) still remains where their apices are not yet worn; and I believe that evidence is not wanting to show that this is the case in all the true elephants. The gradual elongation of the individual cusps of Proboscidiæ is shown in the following seven diagrams (Fig. 3),

selected and reduced from Plates I., II., and III. of Falconer and Cautley's *Fauna Antiqua Sivalensis*.

Fig. 3.



1. Longitudinal and vertical section of the crown of a lower molar of *Dinotherium magnum*.
 2. Same of two cross-crests of an upper molar of *Mastodon ohioiticus*.
 3. Same of two cross-crests of a lower molar of *Elephas ganesa*.
 4. Same of three cross-crests of *E. insignis*.
 5. Same of a cross-crest of *E. plantifrons*.
 6. Same of a lamellum or cross-crest of *E. hysudricus*.
 7. Same of *E. indicus*.
- d, Dentine; e, enamel, and c, cementum.

As we have seen, the increase in mass and length of the food triturating organs (teeth) of herbivora have increased as we ascend through the successive geological horizons, have uniformly been broadened to present a more available crushing surface, and have, in many special cases, diverged from the ancestral type, apparently because certain strains operate in a way entirely new, owing to the necessary, voluntary, or intelligent assumption of new habits of life. I would add the following from unpublished MS. upon another subject: "When the various groups of terrestrial running birds and mammals, and also the saltatory, or leaping mammalia, are considered, the evident strengthening and modification of certain toes, resulting in their specialization and

reduction, is so apparent, that to deny the agency of strains as a very potent cause, is simply to ignore the plainest principles of physical development, where to accelerate that development, gradually increasing resistances must be overcome so as to acquire increased strength, as illustrated in the training of oarsmen, gymnasts, lifters, and pugilists. The peculiarities of muscular development, induced by peculiar strains incident to the pursuit of certain trades, is a further illustration.¹

As it is by the duplication of tubercles in various directions, their fusion, suppression, or atrophy, enlargement or hypertrophy, and total suppression, that the various types of teeth and dentition seem to have arisen, some of the causes of these changes may next be considered. But in order fully to appreciate the potency of such causes as may be suggested, it will be well to take a glance at some of the dental systems of the mammalia to see if there is any evidence of plasticity of the teeth. What favors the idea of plasticity more than anything else is the constant reversal of the forms of the tubercles in opposite molar series, as in Artiodactyls and Perissodactyls, the reversal of the plan of the foldings wherever the ptychodont type prevails, as in rodents and *Toxodontia*, as though forced into those shapes by some force always acting in a definite direction. The fact that the component cusps of the molars of almost all rodents and ruminants are, in the former, transversely, and, in the latter, longitudinally compressed, as though pressures operating in these respectively opposite lines of mandibular movement had induced the compression, is strong presumptive evidence in favor of the doctrine of plasticity of dental structures. I would not so strongly insist upon plasticity in the adult as in the young animal, when the teeth first appear, and when in many cases they are very perceptibly flexible, though very brittle. The evidence which is, however, most striking of all is the gradual derivation of the crescentoid type of cusp, apparently from the conical type. This crescentic form is constantly intensified as the pliocene is approached through the previous geological horizons, as though some force relatively uniform in degree and persistence had been in operation throughout a great length of time, effecting but slight changes towards

¹ A German surgeon, to whose papers I cannot now refer, became expert in indicating the occupation of tradesmen by a study of the differences of development induced by different trades in the superficial muscles.

the later type in a single generation, but entailing that slight change upon offspring through the law of heredity, and these two processes again indefinitely repeated until the sum total of perhaps infinitely slight differentiations effected in this way, amounts to the difference of form we note to-day between the ancient bunodont and modern selenodont.

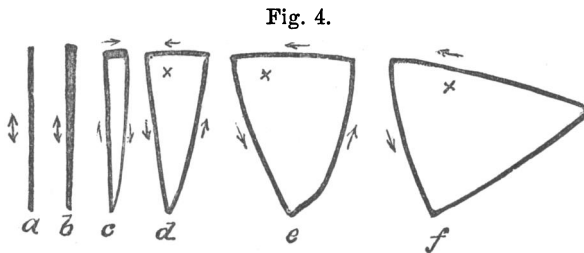
Zoologists, previous to this time, seem to have paid little or no regard to the mandibular movements of animals as the proximate causes of tooth modification. Although most of the reasoning in favor of such a view is of the *a posteriori* kind, there is not wanting in other facts of biology the obvious relation between cause and effect, which is here appreciable only as an effect, for which it is entirely warrantable to assume a cause discoverable, and capable of a rational interpretation. Indeed, until the appearance of the palæontological works of such pioneers as Owen, Leidy, Falconer, and others, it was scarcely possible that anything suggestive of a constantly active modifying force should have crossed the mind of the zoologist. It was from their work, in connection with some studies in recent osteology, that I was led to commence making observations upon the various living groups, as represented more particularly in the collection of the Philadelphia Zoological Society,¹ with especial reference to the kind of mandibular movement peculiar to the different orders, and I was not disappointed to find my surmises substantiated by the actions of the living animals. I observed that there were several distinct kinds of mandibular movement, each kind corresponding to some very distinct type of tooth, which led to the observance of other classes of facts, whose import, until then, I had not comprehended. I noticed, too, that in some cases the movements were different at different times in the same animal, and in some that the kind of movement during rumination was characteristic of a single species, as in the camel.² I also noticed that the lamas and vicuñas had peculiar movements, which seemed to be transition forms, imperfectly bridging the gap between that characteristic of the camel and the ordinary type of ruminants.

¹ I take this opportunity of making an acknowledgment for the facilities so kindly afforded to me for study by Mr. A. E. Brown, the Superintendent of this institution.

² This feature is as characteristic of the *Tylopoda* as the synchronous forward movement of both legs one side in walking.

In no case, however, did the movement depart from the kind characteristic of the species, family, or order, so as to invalidate any conclusions which might be drawn from them as conditioning changes in tooth-structure. Due allowance was also made for the different kind of food which, in special instances, the creatures under consideration were compelled to eat in confinement, due to removal from their native wilds.

The varieties of mandibular movement observed are diagrammatically shown in Fig. 4, which were obtained by selecting and



watching some point on the end of the mandible, or of the lower lip while the jaws were in motion, and the various figures which were thus described by the point chosen were found to be in various animals very nearly those marked *a*, *b*, *c*, *d*, *e*, and *f* in the diagram. The end of the mandible in carnivora was found to describe that at *a*, this was also noticed as the characteristic figure described by the pigs, and, for theoretical reasons, is assumed to be characteristic of the *Hippopotamus* and the earlier types of ungulate mammalia. In the feline section of the carnivora no other kind of mandibular movement would be possible, since, as has been noticed, the descent of the anterior and posterior bony borders of the glenoid cavity is such as to grasp the cylindroid condyle so as to constitute the most strongly marked type of ginglymoid mandibular articulation in the class, though there is some approach towards it in the bats. The gradual departure from this extreme type of mandibular articulation through the dogs, hyenas, and bears does not affect the kind of figure which a certain point at the end of the jaw will make in these cases. The movement which produces *a* is that made in simply opening and closing the mouth, and the whole process of mastication is effected in this way in dogs, cats, pigs, hippopotami, bats, opossums, and all other

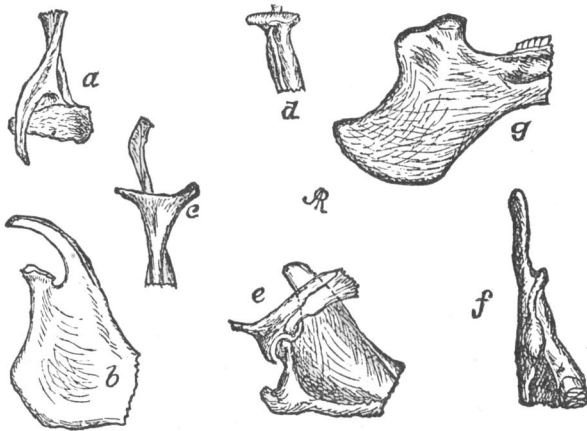
bunodonts or their immediate allies. The figure *b*, showing slight lateral movement, is that made by *Phacochærus*, which is one of the few pigs in which the teeth become worn perfectly plane on the crowns, the surface of which is at right angles with the vertical axis of the tooth. That at *c* is the figure described by the tip of the mandible of the Tapir while feeding on hay and fresh grass, showing that the texture of the aliment makes no change upon the jaw movement. Fig. 4, *c*, may also be regarded as typical, with slight modification (a little oblique), of the kangaroos and phalangiers; the molar teeth of which, also, strongly remind one in some respects of those of the tapir. At *d* a theoretical form is shown, so as to fill the gap between *c* and *e*, and which, no doubt, was exhibited at some stage of the transition from *c* to *e*, *Anchitherium* might be suggested as a probable case. That at *e* is the figure observed in many species of both ruminants and non-ruminating creatures. Several of the *Cervidæ* and the rhinoceros were observed to describe this kind of a figure, and from its prevalence amongst ruminating animals, which I had the opportunity to notice, I suspect that it is the commonest form. The figure at *f* is that described by the giraffe, camel, and ox, in which the extreme in respect to the degree of lateral excursion is also reached.

In respect to the movement of other groups, such as the rodents, for instance, the movements were made with such rapidity that it was with great difficulty that the form of the figure described by some fixed point at the end of the mandible could be seen plainly enough in the absence of a more perfect recording apparatus than the eye of the observer. Enough was made out, however, to show that the motions were often similar to those in the ungulates; this was especially observed in the rabbits and guinea pigs, where an alternate movement of the mandible was made first towards one side and then towards the other, as in the camels. In *Geomys*, *Arvicola*, *Fiber*, and numerous other rodents, the motion of the mandibles when in contact, is believed to be from before backwards, on account of the direction of the flexure of the molars, and the absence of cross-crests on their crowns. In the elephants, however, it seems to be from behind forwards, just the reverse of that noticed amongst some of the rodentia with the absence of cross-crests, as in most of the latter.

It was this absence of cross-crests in the rodentia, together

with the isognathism of the modern elephants, and the presence of salient cross-crests, with a well-marked anisognathism in *Trilophodon*, *Tetralophodon*, *Stegodon*, and *Dinotherium*, that has led me to infer that the mandible was moved from side to side in these genera, just the reverse of what is the fact in the former.

Fig. 5.



- a. Condyle and posterior portion of ramus of the mandible of Giraffe from above.
- b. Same, external view.
- c. Same, posterior view.
- d. Same of wild cat, inferior view.
- e. Wild-cat, side view.
- f. Same of *Hydrochaerus* (water-hog), superior view.
- g. Same as f, from the side.

As some points in relation to the condyle and mandibular articulation were discussed at the outset, I have thought it advisable to figure some of the most distinct forms of this part, as seen in widely separated groups. Fig. 5 represents the condyles of the mandibles of the giraffe, wild cat, and water hog. At a, b, and c, one of the condyles of the giraffe is seen from the above side and from the rear, respectively; it is seen to be greatly elongated transversely, and internally concave from side to side, perfectly flat upon the outer two-thirds of its articular face. We may associate this type of condyle with the kind of figure described by the movement of this creature's mandible in Fig. 4, f, or, we may state it as a principle, that, where the condyle is greatly elongated transversely and very flat, there is

great lateral excursion, during mastication, with selonodont molars, and a great degree of anisognathism. It must not be forgotten, however, that the type of condyle found to exist where the lateral movement of the mandible is not so extensive, is also less flattened and not so much elongated transversely, as will be seen in the Tapir (see Fig. 4, *c*, for diagram of the movement). In the rhinoceros (Fig. 4, *e*) the condyle is also less modified on account of the lesser lateral movement.

In the cats the characteristic cylindroid condyle (Fig. 5, *d*), and the processes that partially clasp it anteriorly and posteriorly, are shown in Fig. 5, *e*; again enforcing the relation subsisting between condylar structure and jaw movement, Fig. 4, *a*. Here again, as in the previous case, the structure is modified, as we pass from the most specialized carnivorous group, cats, to the less specialized dogs and seals, where the anterior and posterior processes from the anterior and posterior boundaries of the glenoid cavity are less salient. The idea has suggested itself to me from seeing the different modes in which the two groups, cats and seals, feed, that the differences in the structure of the mandibular articulation may have something to do with the manner in which they tear their food into pieces small enough to swallow. The cats hold the prey with the fore-feet, the incisor and canine teeth are fastened upon some part, while the paws, with the aid of the retractile claws, hold the prey securely down; the head is then raised and thrown back, and in this way the tough ligaments, tendons, integuments, and muscles are torn apart into pieces sufficiently small to be further acted upon by the molars and swallowed. The seals, on the other hand, fasten the teeth upon their prey (if a fish, always head first), and with sudden lurches of the head and body sidewise, with surprising velocity, the fish is torn in two by means of the suddenness of the movement, the free end being thrown several feet away, which is, however, very soon recovered, and, if too large to swallow whole, is treated as before. Now in the first case the strain incident to pulling back the head by a number of powerful muscles, while the prey is held with the paws, must tend to pull the condyles of the jaw out of the glenoid cavities, which is prevented by the nature of the mandibular articulation. In the case of the seals the method involves no forward pull upon the jaws, but a principle in natural philosophy is taken advantage of, by which, with no more expenditure of force,

the same end is attained as by the cat. The sudden lurches give the mass of the fish a great momentum, which is suddenly arrested, resulting in its breaking in two, when, with little chewing, the piece held by the teeth is swallowed, the throat seeming to be surprisingly dilatable. By what process a seal was ever capable of fathoming any principle of physics is more than I propose to explain, but such are the facts. It may be added that what holds in respect to habits of tearing the food in the cats, also holds in respect to the bears, weasel family, and raccoons, and in a less degree in the dogs and hyenas.

The condyle in the *Hydrochærus* is exceedingly elongated, the antero-posterior diameter of the condyle proper exceeding twice its transverse diameter, which fits into a groove-like glenoid cavity, looking somewhat as though it had been cut out with a rabbet plane. The sides of the groove are vertical, and at right angles to the bottom; it is also longer than the condyle proper, which is not by any means neatly adapted to fit it as is usually the case. So marked is this artificial appearance that the first time I beheld it I made a careful examination to see if some one had not been carving it into what I thought was a fanciful shape, as a trick to deceive. When the reversed inclination of the teeth above and below is noticed, together with the insertion of the muscles, it is plain that the condyle has a reciprocating motion in this groove (glenoid cavity), which goes a great way in explanation of the shapes of the teeth of certain aberrant groups of rodents. Indeed I am satisfied, from the manner in which certain rodents feed, and the way in which their scalpriform incisors are inserted with the direction of their curve, that no other arrangement would answer, since the jaw could not be sufficiently retracted, as in the case of the beaver, to take between his incisors the great breadth of chip which he is able to cut at one bite.¹ I have measured single tooth marks of this animal in wood $1\frac{1}{2}$ in. long.

Relation of the Lateral Excursion of the Mandible to Anisognathism.—As I have previously remarked that anisognathism was an invariable accompaniment of lateral movement, it now remains to substantiate this assertion by the following table. Bunodonts, which stand first, may be set down as unmodified, while sym-

¹ See Morgan, "The American Beaver and his Works," Lippincott & Co., Phila., 1868, p. 176.

borodonts, selenodonts, and tapirodonts, may be regarded as representing the extremes of dental metamorphosis due to the persistent action of the forces exerted in mastication by these latter, and which have been operative since the appearance of the herbivora, the time of which I do not propose to indicate even approximately.

	Upper molar series.		Lower molar series.	
	Anterior.	Posterior.	Anterior.	Posterior.
BUNODONTS.¹	mm.	mm.	mm.	mm.
Hippopotamus amphibius16	.101	.15	.107
Chæropsis liberiensis078	.07	.74	.069
Babirussa alfurus059	.04	.052	.039
Sus indicus068	.043	.068	.049
Dicotyles torquatus049	.043	.049	.038
Phachærus æthiopicus069	.055	.065	.047
SELENODONTS.				
Titanotherium prouti253	.117		
Helladotherium duvernoyi206	.104		
Anthracootherium magnum08	.034	.056	.034
Sivatherium giganteum219	.139		
Equus caballus127	.085	.095	.062
Gazella euchore062	.031	.039	.024
Connochætes gnu089	.047	.059	.041
Alcelaphus caama081	.052		
Capra hircus06	.035	.037	.028
Ovis montana ♂072	.045		
Ovis aries069	.044	.049	.031
Cariacus columbianus068	.045	.049	.033
Cervulus sp. . .	.059	.038	.046	.03
Alce malchis ♂137	.088	.103	.058
Antilocapra americana072	.049	.052	.034
Rangifer tarandus091	.069		
Cervus canadensis115	.075	.085	.058
Camelus dromedarius112	.052	.095	.042
Auchenia glaama073	.031	.05	.028
Camelopardalis giraffa123	.077	.089	.047
Bos taurus137	.103	.099	.077
Oreodon major081	.047		
Rhinoceros indicus158	.09	.124	.081
TAPIRODONT.				
Tapirus americanus096	.055	.087	.05

¹ The measurements were made from the external borders of the crowns of the molars of one side to the external borders of the crowns of those of the other side, at the anterior and posterior ends of both the upper and lower series.

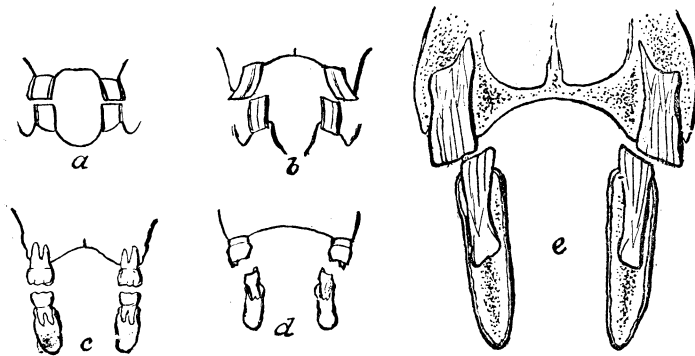
	Upper molar series.		Lower molar series.	
	Anterior.	Posterior.	Anterior.	Posterior.
TRICHECODONTS.	mm.	mm.	mm.	mm.
Manatee australis037	.039	.034	.03
Halmaturus dorsalis033	.022	.028	.02
Petrogale penicillatus028	.018	.023	.018
Phalangista vulpina025	.022	.022	.017
Hypsiprymnus cuniculus02	.015	.017	.012
RODENTIA.				
Sciurus, sp.014	.012	.013	.01
Spermophilus, sp.0135	.011	.012	.011
Cynomys ludovicianus021	.019	.018	.016
Arctomys monax027	.0225	.026	.023
Tamias, sp.008	.007	.007	.006
Hydrochærus capybara055	.024	.057	.033
Castor fiber032	.024	.027	.019
Geomys bursarius01	.0015	.0105	.009
Mus rattus008	.0075	.009	.008
Neotoma01	.009	.01	.009
Sigmodon hispidus0085	.007	.008	.007
Fiber zibethicus013	.013	.013	.013
Hystrix cristata027	.026	.026	.024
Lepus cuniculus023	.021	.018	.015
Cælogenyx paca027	.026	.026	.023
Lagostomus trichodactylus027	.022	.029	.015
Dasyprocta, sp.022	.022	.018	.016

I append a series of similar measurements of primates, to further enforce the idea that selenodont cusps are an accompaniment of anisognathism and lateral movement. The anisognathous extreme is put first in *Aluatta*, or howling monkey, as an example; the isognathous last, as in man.

	Upper molar series.		Lower molar series.	
	Anterior.	Posterior.	Anterior.	Posterior.
	mm.	mm.	mm.	mm.
Aluatta, ♂043	.03	.039	.025
Cynopithecus, ♂046	.041	.042	.036
Gorilla, ♀055	.054	.048	.048
Chimpanzee064	.06	.055	.051
Australian, 1827. ♂, Port Philip, New South Wales067	.06	.067	.048

At Fig. 6, diagrammatic, transverse sections through the jaws of several genera of mammals are shown: *a*, shows the isognathous arrangement in *Fiber zibethicus*; *b*, the anisognathous arrangement in *Lepus cuniculus*. These two show the extremes in rodents; in the first, the teeth of both sides are perfectly parallel; in the latter, neither are they parallel, nor are the series of molars in opposite sides of the upper and lower jaws separated by the same interval. *Fiber*, in some respects, calls to mind the dentition of bunodonts, while *Lepus* reminds one of the selenodont system. The differences are here to be regarded as arising, in a large measure, from the strains incident to mastication, as the contact of the upper and lower molar teeth of *Lepus* always takes place first upon the outer portion of the crown of lower ones, and the inner portion of the crown of the upper ones; and after contact the movement of the jaw is from within outwards, causing the upper molars to be pressed outwards, and the lower molars inwards, eventually causing the upper series to recede from each other, and the lower series to approach each other, probably carrying the rami along in the changes. Nor does the change stop here. The molars are apparently curved outwards above and inwards below from the same cause.

Fig. 6.



Cross-sections through the maxillary apparatus of:—*a. Fiber.* *b. Lepus.* *c. Dicotyles.* *d. Cervus.* *e. Equus.*

The movement in *Fiber* is totally different, though at times there are indications of lateral movement. It seems to be from before backwards, or a reciprocating movement.

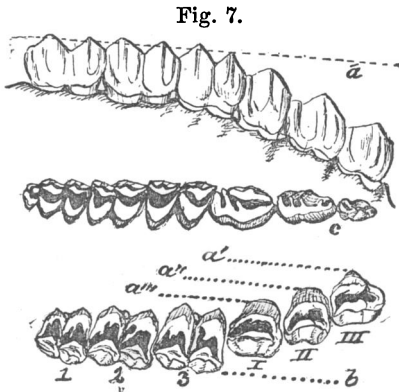
In Fig. 6, *c*, we have a diagram of a transverse section of the jaws of *Dicotyles*, where, as in *Fiber*, the series are nearly parallel in both jaws, and nearly exactly isognathous; the jaws open and close without a particle of lateral motion. The food, in such a case, is pounded as in a mortar, with a chopping motion of the jaws. The anisognathous arrangement is represented in Fig. 6, *d*, of *Cervus*, and *e* that of the horse; both have extensive lateral motion, with corresponding anisognathism; the teeth are also, to some extent, inclined outwards above, and inwards below, as observed in regard to the dentition of *Lepus*. The method of trituration is also very different from *Dicotyles*. It is here ground as in a mill, the reversed enamel patterns of the opposing molar series simulating most closely some of the mechanical devices used by man as grinding mills. The lower jaw, with its molars, however, represents the millstone, and the upper the "bed-stone" or surface upon which it acts with the glenoid cavity as the point from which its oscillations are propagated.

From the preceding tables of measurements the work of constructing a series showing the relation of mandibular movement to anisognathism would be an easy task; the movements would in every case have to be observed, and in all cases where I have been enabled to do so I have found this relation to subsist. We are met, however, by a most anomalous type of anisognathism amongst the cavys, especially in *Cælogenys paca*, where the interval between the molars of opposite sides is greater for the lower series than for the upper. The molars are, however, extensively curved outwards above and inwards below. Indeed, the degree of this curvature is more extensive in the molars of this animal than in those of any other mammal with which I am familiar. What the original relative position of these teeth may have been in their ancestry I do not know; but it is plain that, if this curvature had not taken place, the process of mastication could not be accomplished at all, since, if the teeth were straight, they could scarcely be brought into adequate contact by even the most extensive lateral mandibular movement with which we are acquainted. It seems to me to be a fair inference that they were isognathous, as most of the earlier forms seem to have been, and that some cause—most probably the strains incident to mastication—has been operative in inducing the change to the present form.

There is evidence in the enamel foldings to show that the same kind of strains were operative here as elsewhere.

A matter which has considerable interest in this connection, is what I have ventured to call *displacement due to strains*. The evidence is met with all through the anisognathous artiodactyla and periosodactyla. The relative position of the molars and pre-

molars in *Cervus* is shown in Fig. 7, *a*; the molars, 1, 2, 3, are directly behind each other; they seem to have been shoved from the line *a'* through *a''* and *a'''* until their outer borders have reached the line *b*; the premolars, I., II., III., have meanwhile been left with their inner faces touching respectively the lines *a'*, *a''*, *a'''*. The outer faces of the premolars are parallel to the line *b*, as though the displacing force had acted

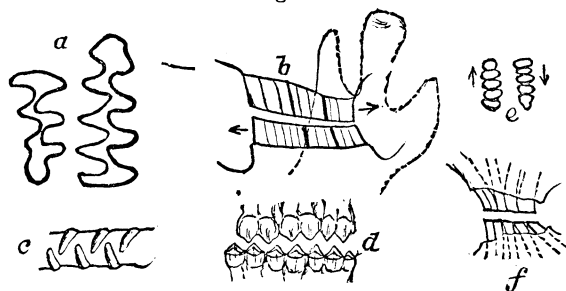


Upper figure, external view of upper molars of *Cervus*. Middle figure, lower molar series of right side of same, not displaced, and lower figure, left upper molars of same, greatly displaced.

equally upon the anterior and posterior portions upon the inner side. This displacement is uniformly the greatest in the later forms, most anisognathous, and with greatest lateral excursion of the mandible. In the molars of the mandible, *c*, no such displacement occurs as noticed in the upper molars; the reason seems to be that the lower teeth, confined as they are to the narrow ramus, cannot undergo such displacement. The force of the mandible always acting to push the upper teeth outwards, since they always first come into contact upon the inner border of the crowns of the upper molars and the outer of the lower ones, would also react powerfully, during mastication, upon the lower molars, tending to push them inwards, and approximate the series (rami) of opposite sides. The molar series of the mandible of the giraffe are, as a whole, slightly convex internally; the reverse of the upper series, which is convex externally. The reversal of this convexity is in keeping with every other character. The displacement seems to be greatest where the masticatory muscles

can act with the greatest force—that is, nearest the articulation of the mandible with the skull. Amongst rodents having a reciprocating motion of the mandible this displacement of one part of the series, while others remain undisturbed, is not very great where only the backward and forward reciprocating movement is present, but sometimes lateral movements are also executed which causes displacement in two directions in both upper and lower molar series. Usually the changes could not be called displacement, but rather a bending or deflection of the teeth in two directions, either backward and outward, or forward and inward. The first condition is usually found in the upper molars, and the second in the mandibular molars of rodents.

Fig. 8.



a. A last upper and a first lower molar *Arvicola*. *b.* Diagram of molars of *Fiber*, showing plane triturating surface of molars. *c.* Undifferentiated hadodont teeth of *Delphinaus*. *d.* Diagram of an opposing series of one side of *Cervus*, showing the mode of intercalation of cross-crests. *e.* Upper and lower molar series of *Geomys*, showing the first upper and last lower molars more compressed. *f.* Side view of dentition of *Geomys*, showing the implantation and opposite inclination of opposing series.

The obliteration of the transverse crests of the teeth of rodents with reciprocating motion of the mandible is shown in Fig. 8, *b* (*Fiber*); also the opposite inclinations of the upper and lower molars, apparently due to the reciprocating movement and the strain incident to the teeth in the execution of such movement during mastication. The same opposite inclination is observed in the molars of *Geomys* at *f*, but more pronounced. The greater flattening of the columnar molars, anteriorly in the upper series, and posteriorly of the lower series at *e* and *f*, is due apparently to the same cause. At *d*, Fig. 6, the molars of *Cervus* are shown with their deep transverse valleys and cross-crests, showing the persistence of this arrangement where the mandibular movement

is entirely lateral. At *c* the alternating, interlocking, haplodont teeth of *Delphinus* are shown almost entirely prehensile, not having attained the specialization of molars. The recent proboscidi-ans, with their numerous transverse enamel plates, are simply the more compressed, transverse crests of *Trilophodon* and *Tetralophodon* in greater numbers. The crests, in a young state of the teeth, are present, but are afterwards worn off to a common level from the movement of the mandible from behind forwards.

The curious analogy of the method in which the succession and wear of the molars and cross-crests takes place in ungulates and proboscidi-ans is worth noticing; in the former, the first and most anterior true molar is most worn; in the latter, the anterior cross-crests in both mastodons and elephants are the first to be worn, the heel or posterior part of the tooth remaining frequently totally unused. The succession of molars, vertical and horizontal, secures the same results in both. The first true molar of ruminants is the first to be protruded; its anterior pair of cusps, as well as those of its fellows behind, are most worn and longest, so that a mere increase in the number of transverse pairs of cusps heterochronously protruded, would give us practically the same result as the horizontally succeeding molars of proboscidi-ans.

I cannot dismiss this subject without a reference to the skull of an Australian in the Morton collection of the Academy of Natural Sciences of Philadelphia, No. 1327, with 35 teeth, 34 of which are normally arranged, there being a supernumerary molar on each side above. If these had been repeated in the mandible, the dentition would have been as low as that of the South American monkeys. As it is, it is lower than the gorilla and chimpanzee in this respect, and shows the tendency of even primates to revert towards the primitive formula of 44 teeth prevalent in eocene times.¹ The jaws are massive, with a most pronounced pithecoïd squareness in front, its prognathism being in marked contrast with the beautiful orthognathous skull of the European. The point, however, which has a practical bearing, is the fine state of the teeth and their massiveness as compared with the teeth of the

¹ In a skull of *Ateles geoffroyi* from South America, I have observed that there were ten teeth in the upper left-hand maxillaries, a number which, if it had been repeated all round, would have given forty teeth as the formula, which is within four of the archetypal forty-four. Lemurs have the thirty-six, in common with the lower South American monkeys.

higher races. The incisors are fully twice the mass of those of the present man, and the molars show an almost equally great development. In explanation of this we have not far to look. We are informed by various authorities¹ that these people were totally ignorant of boiling, but that everything was roasted, or even eaten raw, which involved more work for the teeth than falls to their lot now-a-days, and which must powerfully react upon their development. If, as we believe, and as the facts warrant us in believing, that the dental armature becomes more massive as strains become more frequent and severe through the passage and survival of herbivorous types from eocene to modern times, it is almost equally certain that, in the event of the introduction of cookery, with its constantly increasing refinements, there must be a diminished amount of strain upon the teeth, tending to cause atrophy or degeneration.

Cusp-Shaping Forces.—We now come to the consideration of the way in which the cusps of the teeth have been modified by the various mandibular movements, culminating in the crescentoid form and its modifications. We have assumed, as we have had evidence for doing, that many of the parts associated in the function of mastication were greatly modified and brought to their present shape by mechanical resistances incident to the performances of such function, our next purpose will be to show that a similar process has been silently and powerfully at work in the shaping of the cusps. I am aware that some of the points taken might be called anatomical platitudes, but I believe also that these same have never yielded the meaning they were capable of yielding, except to one who would coordinate the peculiarities of structure in special cases with their correlative influence upon habit. But in order to induce changes in the mechanical arrangements of the active and passive elements of organic structures some change in a creature's surroundings must take place over which it has no control. Such changes may be specified as meteorological, climatic, floral, faunal, geologic, and telluric. It is scarcely worth while to point out the antagonistic relations which life sustains

¹ Herbert Spencer, *Sociological Tables*, Pt. I. A., Tab. IV. ; and, bearing more or less directly upon this point, see Dr. E. Lambert's paper on the Morphology of the Dentary System in the Human Races, in *Bull. l'Acad. Royale de Belgique*, 46e Année, No. 5, 1877 ; Abstr. in *Am. Journ. Science*, vol. xiv. 1877, p. 323.

to its surroundings since geology and palæontology afford such abundant evidence of the constant struggles on the part of life to cope with the altered conditions. To all acquainted with the leading facts of geographical distribution of animals and plants it is well known that some of the most intimate relations exist between flora and fauna, fauna and fauna, flora and fauna and climate, how that elevation due to geologic changes affects climate, and how that telluric changes (orbital), preponderating over all else, should modify all the others, as Prof. Croll¹ would have us believe.

I believe that the changes in these great elements of surrounding conditions may have been adequate to produce either the annihilation or the divergence and survival of organic types. Those creatures which were not in harmony no doubt were often destroyed in affecting the readjustment, because in some the adjustments could not be brought about quickly enough to prevent the fatal waste of efforts in overcoming greatly unbalanced relations. Those that overcame this readjustment survived with modifications. Then, again, there may have been no sudden modifications, but slow changes to which organisms could readily adapt themselves; and, again, there is no telling how much intelligence may have had to do in the struggle, yet there is very little that can be predicated in respect to this by brain-bulk, because if such instances as the beaver, the bee, and the ant are cited, it is at once seen that, even supposing the bulk of brains to augment as recent times are approached, it is not altogether safe to lay too much stress upon brain-mass as an index of intelligence.

The divergence of the educabilian orders of mammalian vertebrates from a forty-four toothed bunodont type with five toes is held by the most eminent authorities. The prevalence of these two characters in eocene mammalia with their gradual disappearance through later forms is one of the strongest arguments in favor of the theory of descent. The gradual increase in the length of the diastemata between molars and incisors from none at all in many eocene forms to the immense interval between the two in such forms as the horse and giraffe is the first point. Another is the prevalent departure from primeval pentadactylism towards monodactylism, or its equivalent, by the fusion of one or more

¹ Climate and Time, Jas. Croll. London, 1875.

parts into a single one, as, for example, the horse and artiodactyl ruminants. The tendency to monodactylism, it is believed, is due to the strains incident to locomotion affecting the growth and nutrition of these parts. It would, therefore, seem that, considering the weight of opinion upon the origin of diastemata and monodactylism, that the teeth should likewise, as characters of secondary morphic and systematic value, and so admirably conditioned for great modification, manifest very sensibly the influence of such conditioning forces.

If environments affect choice of food, etc., it must follow, as a necessary consequence, that different methods of prehension and comminution must be employed in different animals to correspond with the nature of the food, which would effect corresponding dental differentiations. These, in turn, make further differentiations, which are successively fixed by the law of heredity, less difficult in succeeding generations, until extremes are reached. This is just what we have tried to show in the two extreme types of mandibular movement, vertical and lateral, and that the former passes gradually into the other just as it can be shown that the bunodont type of tooth gradually passes into the selenodont. Two or three stages of cusp modification are sometimes observed in the same tooth, while as many as six or eight or more tooth modifications may be counted in the teeth of the whole series.

Odontomorphic Centres.—While making measurements of the skulls in the collection of the Academy some curious facts were elicited. It was observed, that, if a pair of dividers were taken, placing one point on the glenoid cavity of the skull or condyle of the mandible, the curvature of the cross-crests and intervening valleys of the molars of the same side would exactly coincide with that produced by a sweep of the free point of the dividers across them. The same rule was found to hold good in regard to the other side of the skull. We were not long, however, in finding that this rule was not universal among selenodonts; that there were some in which such a coincidence could not be obtained by the method described. It was then observed in these other cases that, if one leg of the dividers was placed on the posterior end of the basi-sphenoid bone, opposite to and midway between the glenoid cavities, for the superior molar series, and midway between the condyles for the mandibular molars, the arc described by the point of the free leg would now coincide in the curvature

with the cross-crests and bottoms of the valleys of the molars of both sides when produced across their crowns.

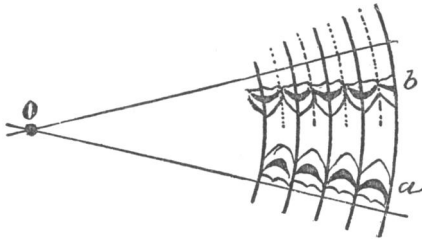
It is proposed for convenience to designate the teeth, the cross-crests of which coincide in curvature with arcs described respectively from the right and left glenoid cavities as centres, for the molars of these sides respectively, as *biaxial*; and those where the centre of this coincident arc is medial on the basi-sphenoid bone, or midway betwixt the condyle, as *uniaxial*. The centres may be named odontomorphic, or tooth-shaping, since they are the fulcra which control the forces which slowly modify the shapes of the teeth and their component tubercles. The biaxial molar is by far the commonest. I have observed it in the following orders: Edentata, Sirenians, Proboscidiens, Rodents, Perissodactyles, Artiodactyles, Hyracoidea, and Marsupials. The following is a list of some of the observed genera of both classes:—

<i>Biaxial.</i>	<i>Uniaxial.</i>
Ovis.	Tragulus.
Alce.	Hyomoschus.
Cervus.	Moschus.
Antilocapra.	Amphitragulus.
Alcelaphus.	Leptomeryx.
Antilope.	
Gazella.	
Auchenia.	
Camelus.	
Sivatherium.	
Bos.	
Titanotherium.	
Equus.	
Tapirus.	
Phalangista.	
Phascolumys.	
Trilophodon.	
Nototherium.	
Megatherium.	
Hyrax.	
Dasyprocta.	

It will be observed that the *Tragulidæ* monopolize the uniaxial plan, though *Cervus columbianus* is very nearly uniaxial.

In Fig. 9, representing diagrammatically the mechanism of mastication in selenodonts, the curvilinear path of the excursion of the mandibular series of molars, as well as the reversal of the selenoid

Fig. 9.



Ideal diagram, showing the mode in which the lower molar series, *a*, sweeps over the upper series, *b*. The movement being constantly regulated from the mandibular articulation, or odontomorphic centre, *O*.

cusps of the upper and lower series respectively with the ideal odontomorphic centre, *O*, in the mandibular articulation, the gist of the whole matter of tooth modification becomes plain. It is observed that opposite those parts which have the greatest transverse diameter, or which are strongest of the opposing series,

b, impinge upon their fellows, *a*, of the opposite series at the weakest points, or those parts having the least transverse diameter, and *vice versa*. It looks as though the strains incident to mastication has pressed the sides of the cusps of the teeth flat, and curved their cornu outwards in the upper series, and inwards in the lower, by the oft-repeated excursion in one direction. The action of the parts in life appears to be constant, that is, the molars of the mandibles of the right side always moving outwards when crushing the food, and the same of the side opposite. The movements are often, for many minutes in succession, made in the same direction, then in the other. It is found, upon careful observation, that the animal chews upon one side at a time, changing to the other apparently for the purpose of resting. This also accords with the observations of physiologists, that the salivary glands of opposite sides in ruminants and other herbivora perform their function alternately with greater vigor, depending for their periods of activity and repose upon the alternate use and disuse of the teeth of the corresponding side in mastication.

Fig. 10.



A series of tubercles are sketched in Fig. 10, showing the gradual transition from the unmodified bunodont, *a*, to the ex-

treme selenodont, *e* and *f*. The cusp, *a*, is the type observed in the early Miocene genus *Entelodon*, or in *Pliolophus* of the Eocene; *b*, an external cusp of an upper molar of *Leptochærus*; *d*, an external cusp of an early ruminant (*Oreodon*); *e*, outer and inner anterior cusps of a young *Cervus*, shortly before protrusion from the alveolus; and *f*, a premolar of *Coryphodon*. A host of additional examples might be given to enforce the idea meant to be conveyed, but which would simply be repeating with another series of species what has already been indicated, and which can be fully confirmed by reference to works of Leidy, Kowalewsky, and Cope on Tertiary mammalia.

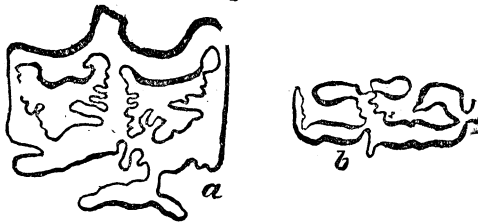
I am aware that *Coryphodon* is an early form, occurring in the Eocene formation, and is perhaps not as well chosen a case to illustrate the modern extreme as might have been selected. This is, however, a superficial objection, since the crowns are very short, with the short roots characteristic of the mammalia of early periods. It seems to be simply a case in which the modifications took place with greater rapidity than in later species. If the whole order of ungulates did not concur in the evidence which they yield, an objection might be raised, but in all of them the reverse direction of the cornu of the cusps of opposing series is the same; in all the mandibular movement is either lateral, or becoming so; almost every family of them shows a progressive intensification of these characters, and it would seem that no further evidence were needed to show that *the necessary actions of an animal modify most profoundly the form of even the very hardest of its tissues*.

It is proposed to close the discussion with the consideration of a few special cases of the various methods of cusp-blending, wear, and flexure. In all the selenodont mammals the flexure of the cornu of the inner cusps and their lengthening in the upper molars and the outer below is greatest, evidently due to the fact that the strains incident to mastication are more powerfully exerted upon these, and less powerfully upon their fellows on the opposite side of the tooth. The deep flexure of the enamel layer, vertically and medially on the inner side of the upper molars and the outer of the lower ones, is another fact to be noted in many instances as due to the same causes. The jutting outwards of the cornu of the external cusps of the upper molars, and inwards of the internal

ones in the lower series, is another fact capable of a similar explanation.

I apprehend that the plicate enamel layers in the dentition of the horse, of *Sivatherium*, and to some extent in the ox and deer, may be accounted for in the same way; for in these the plication is most marked at such points as are manifestly, according to our theory, subject to the severest strains. In Fig. 11, *a*, the enamel

Fig. 11.



pattern of the upper molar of *Equus excelsus*, and *b*, the enamel pattern of an undetermined species of horse (both from Leidy), show this plication of the anterior and posterior transverse enamel walls of the islands in a marked degree. The plication is greatest in a line parallel with the direction of the strains exerted during mastication. Another circumstance is the greater inclination of the inner cusp of the upper molars outwards, and of the outer ones below inwards, which is so common amongst selenodont ungulates, that I think it is almost without exception. The great width also of the posterior molars in selenodont mammals may be accounted for in a great measure by supposing molar force as adequate cause of such increased transverse diameter. This view is supported in a measure by the relatively equal transverse diameter of the molars at both ends of the series in bunodont, isognathous mammals. There seems to have been a phylogenetic metamorphosis of molars and premolars, which proceeded with greatest rapidity nearest the mandibular articulation, where the modifying forces were also applied with the greatest mechanical effect. The mandibular masticatory apparatus of mammals may be regarded as levers of the third class, in which the glenoid cavity is the fulcrum, the muscular force exerted by the masticatory muscles the power, and the resistance of the food to the teeth in crushing it the weight. Since the coefficient of muscular force is 104 pounds

per square inch of transverse section,¹ it is easy to surmise what would be the tendency of the exertion of the force of many square inches in section of masticatory muscle upon the jaws and teeth in mastication. It would manifestly not be consumed in the mere comminution of the food, but it must also react upon the structures which were directly subjected to the resulting strains, viz., the teeth. In a mammal as large as the rhinoceros the area occupied by the mandibular teeth is about 5 square inches, while the maxillary teeth occupy about 10 square inches, as I have roughly estimated from a skull nearly adult; the ratio then of the triturating surfaces of the upper and lower series is about as one is to two. These ratios increase apparently as anisognathism increases, and conversely become equal as isognathism prevails; that is, we may select a perisodactyl, such as the rhinoceros, or an artiodactyl, such as *Bos*, to represent one extreme, and the universal pig as the other.

It will be observed that I have made no attempts at constructing phylogenetic tables, a favorite pursuit with some recent naturalists; this is because I am not satisfied in regard to the value of characters as indicating affinities. I appreciate these most thoroughly, but believe that modifications may be greatly accelerated or retarded by alterations in surroundings over which a modifiable organism has no control, so that the differential effects (generic and specific characters of systematists), produced in a given time, may differ greatly in value—their true value being estimated in terms of force—some requiring but half as much time for their production as others. The possible morphological effects of like mechanical conditions are illustrated in turtles and glyptodons, where the rigid exoskeleton has caused the originally segmented axial skeleton to show a strong tendency to revert to the primitive homogeneous condition without losing its osseous character. The exoskeleton has in fact partially assumed the part taken by the chitinous envelope in the organization of the *Articulata*. We may regard the relations here pointed out as the complementary principle demonstrating Spencer's theory of the segmentation of the vertebral axis,² because it must be allowed that opposite conditions must produce opposite effects.

¹ Animal Mechanics, Dr. Saml. Haughton. London, 1873, p. 71; The Principle of Least Action in Nature (Three Lectures), London, 1871, p. 10.

² Principles of Biology, New York, 1867.

Appendix on the Atrophy and Hypertrophy of Incisors.—Without stopping to consider the archetypal or normal forms, the principal groups which manifest the extremes of modification of the incisive elements may be tabulated as follows:—

Rodentia.	}	Hypertrophied incisors with special functions.
Tæniodonta.		
Proboscidea.		Greatly hypertrophied, becoming weapons of offence and defence; function assumed by a proboscis.
Dinocerati.	}	More or less atrophied; function assumed by the lips, or a short proboscis.
Rhinocerotidæ.		
Ruminantia.		Upper incisors absent; function partially assumed by the tongue and muscles of the neck.
Edentata.		No incisors; function partially or entirely assumed by the tongue.

As is now believed,¹ the great specialization of the median incisors of rodents is due to the severe work to which they are persistently applied during the phylogeny of the group, but the extreme of hypertrophy is reached in the *Proboscidea*, where it has been so extensive as to render the teeth useless in the performance of their primary function, which has been exchanged for a new one, viz., a defensive function, while the primary one has been assumed by the greatly developed proboscis used both as a drinking horn and as a hand to grasp and wrench vegetable aliment from its attachment and convey it to the mouth. A fact which points to the conclusion that the tusks of the elephant were once functional incisors is the presence of more or less rudimentary bands of enamel on the tusks of several fossil species, apparently the remains of what once were functional parts of these teeth. The difference in shape of the nasal opening, and indeed of the whole anterior portion of the skull of *Dinotherium* and the same parts in the Elephants and Mastodons, renders it very certain that there was a wide difference between the two in the shape, and perhaps also in the length of proboscis. But such differences alone will not account for the evolution of the long prehensile proboscis, nor is the shortness of the neck (cervical portion of the vertebral column), and the accompanying elevation of the mouth from the level of the ground, any help, because these are both effects depending for their origin upon the initiation of the development of such a proboscis. It is, therefore, necessary that we

¹ Tome's Dental Anatomy, Philada., 1876, p. 250.

look in the direction of some earlier and more generalized form as a starting point from which it is possible to derive the organ so characteristic of Proboscidiens. In this position I find I am in accord with Prof. Cope, who has stated his views upon this matter more or less distinctly at several places in his extensive writings.¹ My reasons, based wholly on teleological evidence, for not believing the *Dinocerata* to be in the direct ancestral line which culminated in the elephants, is the presence in the former of a variable number of pairs of horns, and in *Dinoceras* the great pair of upper laniary teeth are written down as canines by Profs. Leidy, Cope, and Marsh, which, with the absence of upper incisors, gives us no probable beginnings that may be regarded as homologous with the tusks of *Elephas*. However, the tusks of *Proboscidea*, as now known from fossil forms, have been extensively modified in size, situation, and direction of curvature. We may state the modifications as to implantation of the tusks (incisors) in the various forms, thus:—

$$\begin{array}{l} \text{Dinotherium, I. } \frac{0-0}{1-1} \\ \text{Mastodon Angustideus, } \left. \begin{array}{l} \text{M. longirostris,} \\ \text{M. productus, etc.} \end{array} \right\} \text{I. } \frac{1-1}{1-1} \\ \text{Elephas, sp. I. } \frac{1-1}{0-0} \end{array}$$

From the tenor of the foregoing facts, I am led to conclude that, with the disappearance of the primary functions of the incisors in Proboscidiens, and their assumption of a secondary defensive one, the proboscis was gradually developed, while the mouth, as it became more elevated from the level of the ground by the shortening of the neck and the assumption of the long, gravi-gradous pillar-like limbs, were assisting factors in the process. Whatever was the cause of the incisors becoming weapons of defence was the cause of the initiation of a process of development of the external nasal organ, resulting in its present structure and importance. There was probably no organ so directly available as what was then a rudimentary proboscis, seeing that all other parts (limbs), probably by reason of the animal's bulk, must sub-

¹ U. S. Geolog. Surv. Terr., 6th Annual Report, Washington, 1873, p. 647; U. S. Geograph. Surv. W. of the 100th Meridian, vol. iv. 1877, p. 282.

serve purposes of locomotion. Further, after once having reached that stage which made the incisors available as weapons, we can understand how the violent uses to which these parts were and are put only served to carry the hypertrophy still further.

The *Dinocerata* and *Rhinocerotidæ* present a case where the partial assumption of the incisive function by a very flexible and powerful lip has reacted upon the development of the incisors, causing them to become rudimentary. I infer from the rather elevated and thickened nasal bones of the *Dinocerata* that these creatures had a long protrusible upper lip, if not a short proboscis, and the observed correlation between such osteological conformation and protrusible lip in living forms is still further evidence; so is the fact that, in a form (*Palæosyops*) allied to the genus *Titanotherium*, the nasals are strongly produced as in the Tapir, to which it is also allied. I think it improbable that *Dinocerus* possessed a prehensile tongue, a view contradicted by the relatively immobile upper lip, with two or three exceptions, of the *ruminantia*, that are similarly without upper incisors. The horse with his prehensile upper lip has not been considered, but we find, upon observation, that the power he exerts with it is very feeble, and acts rather as a collecting apparatus for the purpose of bringing herbage within reach of his incisors, the most complex, with one exception, in the whole mammalian sub-kingdom. The proboscis of the Tapir is likewise only a grasping instrument, and seems to be used solely for the purpose of fetching its aliment within reach of the incisors, which are well developed. It may also be observed that the earlier and more unspecialized forms of hornless rhinoceroses had narrower nasal bones with the incisors more fully developed, with probably less effective grasping lips, similar to the horse.

In the ruminants the absence of the upper incisors seems to me to be correlated with the prehensile tongue, the lower incisors acting as a knife edge, while a bunch of herbage is held fast by bringing the premaxillary pad above down upon it so as to bind it firmly against the lower incisors, when it is readily severed from its attachment by tossing the head forwards and upwards.

The *Bruta* or *Edentata* are by far the most remarkable group illustrating the interdependence of incisors and a prehensile apparatus, which, in this case, seems invariably to be the tongue. In the edentulous ant-eaters of both continents all the teeth are

aborted. A bird-like character is assumed in one instance (*Myrmecophaga*), in which the pyloric end of the stomach becomes gizzard-like, small pebbles being found within. The extinct and recent sloths, as well as armadillos, have long prehensile tongues, which, it is believed explains their want of incisors. Brehm says (*Thierleben*) the tongue of the living sloth is used like a hand, and Owen thinks the tongue of *Megatherium* was prehensile. From what I have seen of living armadillos I have reason to believe that the *Hoplophoridae* were similarly possessed of prehensile tongues. The well-developed hyoids of this group, as Prof. Burmeister¹ has represented them, would also favor this view. It may be objected to our explanation that no fossil *Edentata* have been found *with* incisors, which should be the case if our theory is the correct one; to this we may reply that so far no *Edentata* have been described from South America older than early pliocene, so that we may look with some degree of confidence for the future discovery of forms with the required incisors or their rudiments from the eocene or miocene of that great continent. A group so sharply defined as the *Edentata* will then have shared the fate of some of the others which were considered as isolated, with irreconcilable chasms intervening, until, thanks to the labors of American palaeontologists, such have been in a large measure filled up. That the want of incisors in existing edentates is no proof of their absence in the forms from which they were derived, receives some support from the fact that rudimentary teeth have been found in the embryos of toothless whales, and also, as should be expected in embryo, *Trionychidae*, a low group of the *Testudinata*, if, as has been held, these latter are remotely allied to the toothed crocodilians.

The following summary of the views arrived at in the foregoing pages is offered:—

1. That the earliest and simplest type of mammalian jaw-movement was that in which the mouth was simply opened and closed, without mandibular excursion, and coexistent with the simple haplodont or bunodont molar.
2. That the development of the various kinds of excursive mandibular movement has apparently been progressive.

¹ Anales del Museo Publico. Buenos Ayres, 1866-73.

3. That as the excursive movements have increased in complexity there has been an apparent increase in the complexity of the enamel foldings, ridges, and crests.

4. From the fact that the foldings, etc., have apparently been modified in conformity to the ways in which the force used in mastication was exerted, it is concluded that the various modes of crest and tubercular modification are related as effects to the diverse modes of mandibular movement.

5. It is apparent from the facts presented throughout the context that the mandibular articulations, and correlatively the whole skull, have probably been modified in shape by the movements made by the jaws and the forces exerted in executing them.

6. From the fact that incisor teeth are partially or entirely absent or relegated to another function in forms which have long prehensile tongues, mobile, prehensile lips or proboscides, it is held to be probable that such disappearance of the incisive dental elements is due to the assumption of their function by the prehensile organs indicated.